

Effect sizes and standardization in neighbourhood models of forest stands: potential biases and misinterpretations

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Summary

1. Effects of conspecific neighbours on survival and growth of trees have been found to be related to species abundance. Both positive and negative relationships may explain observed abundance patterns. Surprisingly, it is rarely tested whether such relationships could be biased or even spurious due to transforming neighbourhood variables or influences of spatial aggregation, distance decay of neighbour effects and standardization of effect sizes.
2. To investigate potential biases, communities of 20 identical species were simulated with log-series abundances but without species-specific interactions. No relationship of conspecific neighbour effects on survival or growth with species abundance was expected. Survival and growth of individuals was simulated in random and aggregated spatial patterns using no, linear, or squared distance decay of neighbour effects.
3. Regression coefficients of statistical neighbourhood models were unbiased and unrelated to species abundance. However, variation in the number of conspecific neighbours was positively or negatively related to species abundance depending on transformations of neighbourhood variables, spatial pattern and distance decay. Consequently, effect sizes and standardized regression coefficients, often used in model fitting across large numbers of species, were also positively or negatively related to species abundance depending on transformation of neighbourhood variables, spatial pattern and distance decay.
4. Tests using randomized tree positions and identities provide the best bench marks by which to critically evaluate relationships of effect sizes or standardized regression coefficients with tree species abundance. This will better guard against potential misinterpretations.

Key-words: community dynamics; multiple regression; neighbourhood model; population dynamics; tropical forest.

27 **Introduction**

28 Whether or not conspecific negative density dependence (CNDD) at small
 29 neighbourhood scales shapes species abundances in tropical tree communities at larger scales
 30 is far from resolved and we probably should not even expect the answer to be simple. In
 31 principle, there are several possibilities. First, the strength of CNDD is unrelated to
 32 abundance. Second, the strength of CNDD is negatively related to abundance (strong CNDD
 33 for abundant but weak CNDD for rare species). This would prevent abundant species
 34 becoming even more abundant and thereby competitively excluding other species. Moreover,
 35 it would confer a rare-species advantage and possibly lead to a community compensatory
 36 trend (CCT, Connell *et al.* 1984). Third, the strength of CNDD is positively related to
 37 abundance (strong CNDD for rare but weak for abundant species). This would explain the
 38 rarity and low abundance of the species with strong CNDD and the high abundances of
 39 species with weak CNDD (Comita *et al.* 2010). There remain though two further possibilities
 40 which are that either a mix of positive and negative processes is operating, or the observed
 41 relationships are simply spurious (*i.e.* the result of a statistical artefact).

42 In an empirical study, Newbery & Stoll (2013) showed negative effects of conspecific
 43 neighbours on absolute growth rate of medium-sized trees. The argument was that reduced
 44 growth of an individual tree will – other factors being equal – translate into survivorship and
 45 fecundity reductions and hence affect species abundances. Nevertheless, direct effects of
 46 conspecifics on survival could be more relevant for population dynamics of different species
 47 within communities. Therefore, the tests reported here simulate both individual survival and
 48 growth rate and use a framework of neighbourhood analysis similar to that of Newbery &
 49 Stoll (2013) to show that all possible relationships of the strength of CNDD and abundance
 50 may emerge without any species-specific or effects of abundances. Moreover, we show that
 51 potential biases do not depend on the nature of the dependent variable.

Relationships between the strength of CNDD and abundance were investigated using a simple, spatially explicit and individual-based, model which simulated identical species without any species-specific interactions. Thus, any relationships between the strength of CNDD and abundance in communities simulated under these assumptions would not be expected. Nevertheless, relationships do emerge because of interfering effects of spatial patterns and distance decay (i.e. the functional form relating neighbour effects to distance from focal trees, Fig. 1) and, perhaps more importantly, due to transforming (e.g. log-transformation) and/or scaling (e.g. standardization or z-transformation) of the input variables. For example, if rare species have lower variability in the number of conspecifics in their local neighbourhoods compared to common species, scaling is expected to decrease effect sizes (or standardized partial correlation coefficients) of rare relative to common species, possibly leading to spurious negative relationships between the strength of CNDD and abundances. Scaling is recommended (e.g. Schielzeth 2010) and applied especially in hierarchical Bayesian modelling to speed up or even ensure numerical convergence (e.g. Gelman & Hill 2007).

Motivation to investigate the relationships between the strength of CNDD and abundance more carefully using simulations came from the opposite outcomes of two recent publications. A consistent *negative* relationship between the strength of CNDD (i.e. effect sizes derived from statistical neighbourhood models) and abundance (total basal area of species) in randomization tests was shown by Newbery & Stoll (2013). By contrast, a strong *positive* relationship between the strength of CNDD and abundance was found by Comita *et al.* (2010). Whilst such different results are interesting, and might be explained by different underlying biological mechanisms operating on different species at different locations, before making such a conclusion possible differences arising from artefacts and biases of the statistical methods should first be ruled out.

Materials and Methods

A completely neutral forest without any species-specific effects was simulated. Initial size distributions of individuals (basal area, ba) were log-normal with mean 2 and standard deviation 1, and simulations were initialized with no spatial dependency in individual size. Individuals of 20 identical species with log-series abundances (i.e. 2827, 1408, 935, 699, 557, 462, 395, 344, 305, 273, 248, 226, 208, 192, 179, 167, 157, 147, 139, 132) were placed on plots (200 x 400 m) either randomly or with aggregated spatial patterns. The aggregated pattern was realized by dispersing individuals around ‘parent trees’ (assigned random locations according to a homogeneous Poisson process), using a Gaussian dispersal kernel with mean 0 and standard deviation 3 m. Thus the species distributions were modeled as a Thomas cluster process, which in turn is a special case of a Neyman-Scott cluster process (Neyman & Scott 1952), and this method means species are spatially independent of one another.

Individual survival was simulated in three steps. First, a linear predictor (y) for survival was simulated for individuals within a border of 20 m using the following multiple regression equation:

$$y = \beta_0 + \beta_1 \log(ba) + \beta_2 \sum_r \text{heterospecific neighbours} + \beta_3 \sum_r \text{conspecific neighbours} \quad (1)$$

with β_0 to β_3 the regression coefficients, ba the initial size (basal area) of individuals and the two neighbour terms simply summing the number of heterospecific or conspecific neighbours within a neighbourhood radius (r) of 20 m without taking size or relative size differences between focal individuals and neighbours into account. The regression coefficients were chosen to lead to roughly 50% mortality for each species. Specifically, $\beta_0 = 5$, $\beta_1 = 2.5$, and $\beta_2 = \beta_3 = -0.05$. Second, the linear predictor was converted to individual

survival probabilities using the inverse logit transformation. Third, binomially distributed errors were used to convert the probabilities to the binary variable survival (0's and 1's) by drawing from binomially distributed random numbers. Survival was then used in logistic regressions as the dependent variable. Regressions were run for each species separately. Standardized regression coefficients (b) were obtained from regressions with independent variables standardized (or scaled) by subtracting their mean and dividing by their standard deviation. Unlike in the neighbourhood analysis for absolute growth rate (agr) as dependent variable (see below), fitted neighbourhood radii were fixed for the logistic regressions at 20 m, because best fitting neighbourhood radii for rarer species were sometime smaller than the simulated 20 m radius. To investigate effects of transformations, the same multiple regression approach as described above, but now with log-transformed neighbour terms was used:

$$y = \beta_0 + \beta_1 \log(ba) + \beta_2 \log(1 + \sum_r \text{heterospecific neighbours}) + \beta_3 \log(1 + \sum_r \text{conspecific neighbours}) \quad (2)$$

with β_0 and β_1 as above, and $\beta_2 = \beta_3 = -1.3$. The β 's of the neighbour terms needed to be adjusted in order to maintain 50% mortality. Again, unstandardized (β) and standardized (b) regression coefficients were estimated by logistic regressions (general linear models with binomially distributed error terms). Finally, β_3 and b_3 , as well as variability in numbers of conspecific neighbours within the neighbourhood radius r for each species, were correlated with species abundances (i.e. $\log(\text{number of individuals of each species at the plot level})$).

In the simulations of individual growth, different distance decays and relative size differences were also taken into account because competition is often size- and distance dependent. Size- and distance dependencies could also have been analysed for survival as dependent variable. However, since the parallel analyses yielded essentially similar conclusions, we present analyses with different distance decays for growth only. For each

individual, one single growth increment (absolute growth rate, *agr*) was simulated for individuals within a border of 20 m using the following multiple regression equation:

$$\log(agr) = \beta_0 + \beta_1 \log(ba) + \beta_2 \log(1 + \sum_r ba_{HET} / w) + \beta_3 \log(1 + \sum_r ba_{CON} / w) + error \quad (3)$$

with $w = 1$ (no distance decay), $w = \text{distance}$ (linear distance decay) or $w = \text{distance}^2$ (squared distance decay, Fig. 1). The neighbourhood terms (ba_{HET} and ba_{CON}) summed the basal areas of bigger heterospecific (HET) or bigger conspecific (CON) neighbours within a neighbourhood radius (r) of 20 m. The random error term was $N(0, 0.3)$. Regression coefficients were $\beta_0 = -0.1$, $\beta_1 = 0.3$ and $\beta_2 = \beta_3 = -0.2$. To verify the simulations, test runs with random errors set to $N(0, 0)$ were performed. The simulations were realized using C++ (computer code is given in Appendix A of the supplementary material).

Neighbourhood models (as in Stoll & Newbery 2005) were then fitted to the simulated data over all possible combinations of radii for HET and CON neighbours using R (R Development Core Team 2012) and parameter estimates taken from those models yielding the highest adjusted R^2 -values. Five runs with different seeds were performed and estimates of regression coefficients from best fitting neighbourhood models, effect sizes (Cohen 1988; Nakagawa & Cuthill 2007) or standardized regression coefficients (e.g. Warner 2012) averaged across the five runs. Effect sizes (i.e. squared partial correlation coefficients, $t^2 / [t^2 + \text{residual degrees of freedom}]$, $t = t\text{-value}$) and standardized regression coefficients ($b = \beta$'s obtained from regressions with standardized variables by subtracting their mean and dividing by their standard deviation) were then correlated with species abundances (i.e. plot level basal area, BA, log-transformed). Standardized regression coefficients can also be calculated from unstandardized β 's as $b = \beta * SD_X$, if the dependent variable itself is not standardized (e.g. survival). In the case of continuous dependent variables (e.g. *agr*), however, the

dependent variable itself is often also standardized as well. In these cases, variability in the dependent variable is also involved in standardizing regression coefficients and $b = \beta * SD_X / SD_Y$. In both cases, a positive correlation of b with abundance implies that less abundant, rare species have stronger CON effects – β is more negative – (as in Comita *et al.* 2010), whereas a negative relationship implies more abundant species have stronger CON effects (as in Newbery & Stoll 2013). Note, however, that possible correlations of b with abundance may be biased due to correlations of SD_X (or additionally SD_Y) with abundance. But if β 's are negative, large SD_X lead to more negative b -values and the relationship with abundance may switch direction not because of a difference in the strength of conspecific interactions between rare and common species, but because of differences in the variability of number and abundance of conspecific neighbours. Moreover, because the simulations and analyses for both survival and *agr* as dependent variables are based on a multiple regression approach, the basic consequences described above (i.e. possible biases in standardized regression coefficients because of differences in SD_X between rare and common species) are essentially the same independent of the nature of the dependent variable.

Results

There were no significant regressions for conspecific density-dependent effects (regression coefficient β_3 in Eq. 1) on survival and species abundance (Fig. 2) regardless of whether untransformed or log-transformed number of conspecific neighbours were used to quantify the neighbourhood. However, variability in number of conspecific neighbours was positively correlated with abundance if untransformed (Eq. 1) but negatively related if log-transformed (Eq. 2). Consequently, standardized regression coefficients were negatively correlated with abundance if number of conspecific neighbours was quantified on the untransformed but positively correlated with abundance if number of conspecific neighbours

were log-transformed. Frequency distributions for the rarest ($n = 132$) and most common ($n = 2827$) simulated species on untransformed and log-transformed scales (Fig. 3) demonstrate that log-transforming the number of conspecific neighbours for rare species (small values) expands variability but compresses the variability in number of conspecific neighbours for common species (large values). This variability in number of conspecific neighbours (SD_x) increases from rare to common species on untransformed scales but decreases from rare to common species on transformed scales.

There were no significant regressions for conspecific density-dependent effects on growth (regression coefficient β_3 in Eq. 3) and species abundance (plot level basal area) regardless of distance decay or spatial pattern (Fig. 4). Variation in parameter estimates was largest for squared distance decay and random spatial pattern. Best fitting radii for bigger conspecific neighbours were unbiased in neighbourhood models without distance decay and random spatial pattern (Table 1). However, in the aggregated pattern and with linear distance decay they were slightly underestimated. With estimates (mean \pm SD) of 15.9 ± 2.6 in the random spatial pattern and 14.5 ± 3.2 , the underestimation was more pronounced with squared distance decay.

Variability in local conspecific neighbour density (within 20 m) varied depending on distance decay and spatial pattern (Fig. 5). A strong negative regression with abundance emerged without distance decay in both spatial patterns. With linear distance decay, the regression was not significant with random spatial pattern but still negative in the aggregated pattern. With squared distance decay, the regression switched to positive in the random pattern, but it was not significant in the aggregated pattern.

As a consequence of variation in local conspecific neighbour density, effect sizes (Fig. 6) and standardized regression coefficients (b_3 , Fig. 7) showed various relations with abundance depending on distance decay and spatial pattern. Without distance decay both

effect sizes and standardized regression coefficients were positively related with abundance, regardless of spatial pattern. This was also the case for effect sizes and linear distance decay, whereas standardized regression coefficients were not significantly related with abundance in random spatial pattern but still positively related with abundance in the aggregated pattern. For squared distance decay, both effect sizes and standardized regression coefficients were negatively related with abundance in random spatial patterns but unrelated in aggregated patterns. Apparently, the squared distance decay cancelled the effect of aggregation.

Discussion

The simulations and neighbourhood analyses with individual survival or growth as dependent variable showed that estimates of regression coefficients (β) were unrelated to species abundances independent of transformations, spatial pattern and distance decay — as expected based on the simulations of identical species without species-specific interactions. However, variability in local density of conspecifics (SD_X) showed various relationships with species abundances depending on transformations of neighbourhood variables, degree of spatial pattern and form of distance decay. As a consequence (i.e. $b = \beta * SD_X$), relationships between effect sizes, or standardized regression coefficients (b), and species abundances were either non-significant, positive or negative.

If untransformed scales are used to quantify conspecific neighbourhoods, relationships with variability and abundance are expected to be generally positive (Fig. B2 in Appendix B) at least in the cases and range of abundances investigated here. In these cases, relationships between standardized effect sizes with abundance will be negative. If, however, log-transformed scales are used to quantify conspecific neighbourhoods, relationships with variability and abundance (Fig. B2) can be modified in all possible ways, i.e. be absent, positive or negative, depending on spatial pattern, exact form of distance decay, but also on

whether or not relative size differences are taken into account. There are many and sometimes rather non-transparent possibilities making it very difficult to systematically evaluate the published literature on neighbourhood models and possible relationships between the strength of CNDD and species abundance, especially where details of how variables were handled are incompletely reported, and data have not been archived to allow independent checks.

By using neighbourhood models without distance decay and unstandardized input variables, in single-species analyses, a negative relationship between CNDD and forest-level abundance was found, at least for the first of the two 10-year periods analyzed (Newbery & Stoll 2013). Using no distance decay, yet standardizing before fitting their models, Lin *et al.* (2012) found positive relationships over their dry-season interval. Using an exponential distance decay, Comita *et al.* (2010) centered (subtracted the mean) but did not standardize (divide by standard deviation) their input variables (L. Comita, pers. comm.) and found a strong positive relationship too. Whereas Lin *et al.* (2012) fitted mixed models using maximum likelihood estimation, i.e. without any prior information being involved, Comita *et al.* (2010) used a hierarchical Bayesian analysis with non-informative priors distributed according to the scaled inverse-Wishart function. This conjugate distribution models the covariance matrix of the species-level regression. Nevertheless, both studies did find positive relationships, thereby apparently supporting one another's conclusions.

The specific scale and distribution of the priors used by Comita *et al.* (2010) might have introduced additional critical information that determined in part the estimation of their coefficients, in a similar way as standardization did in our simulations, and may also have done for Lin *et al.* (2012). Gelman & Hill (2007) discuss the use of the inverse Wishart distribution in some detail, and highlight in particular the need to confirm that Bayesian priors are indeed non-informative across the same ranges of independent variables that result

in the posterior probabilities. Dennis (1996) has discussed fundamental issues concerning the use of non-informative priors and Bayesian analysis for ecology in general.

The results of Newbery & Stoll (2013) dealt with effects of conspecific neighbours (as large tree abundance) on growth of small trees, whereas those of Comita *et al.* (2010) concerned conspecific neighbour effects (as either local tree seedling density or tree abundance) on survival of those seedlings. Their result could be more generally important if confirmed to be fully robust to statistical treatment. It might then support the notion that fundamentally different density dependent processes are likely operating at the seedling as opposed to the small-tree stage in tropical forest dynamics (Uriarte *et al.* 2004 a, b; Newbery & Stoll 2013).

Because of conceptual similarities of neighbourhood analyses of Comita *et al.* (2010) and those of others (e.g. Uriarte *et al.* 2004a, b; Lin *et al.* 2012), the analysis presented here could be more widely relevant. Since standardization can lead to spurious relationships between CNDD and species abundances, its potential influence needs to be carefully considered when interpreting relationships of small-scale effects of conspecific neighbours on larger scale abundance patterns within diverse tree communities. Similarly, care should be taken when specifying and justifying prior information in hierarchical Bayesian analyses. Our recommendation, following from Newbery & Stoll (2013), is that tests that randomize tree positions and identities indeed provide the best benchmark by which to critically evaluate and judge relationships between effect sizes, or standardized regression coefficients, and tree species abundances.

Acknowledgements

We thank the Editors and M. Uriarte for comments on earlier drafts of this forum article.

Supplementary Materials

Appendix A

Documented computer code used for the simulations. A detailed description of input parameters and simulation output is provided in the file named growth_files.rtf.

Appendix B

Relationships of variability in local neighbourhoods with species abundances in different competitive scenarios, spatial patterns and various distance decays.

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TABLE 1. Average best fitting radii \pm standard deviation (SD) for bigger conspecifics in neighbourhood models (Eq. 3) across 20 species with identical initial size distributions and log-species abundances and random or aggregated spatial patterns.

Distance decay	Spatial pattern					
	random			aggregated		
no	20.0	\pm	0.0	19.8	\pm	0.4
linear	19.6	\pm	0.5	19.1	\pm	1.0
squared	15.9	\pm	2.6	14.5	\pm	3.2

Figure legends

Figure. 1. Distance decay of neighbourhood effects. In the cut-off model (dashed), the sizes of bigger neighbours with a distance $<$ cut-off are summed. In the linear distance decay (black), the sizes of bigger neighbours are weighed by $1/\text{distance}$. This is similar to an exponential distance decay (red), which, however, gives somewhat more weight at intermediate distances. A decay of $1/\text{distance}^2$ (blue) yields a very rapidly decreasing function. Beyond 20, all three functions give essentially zero weights.

Figure. 2. Regressions of conspecific effects (regression coefficient, β_3 in Eq. 1) on individual survival, variability in number of conspecific neighbours within neighbourhood radius ($r = 20$), and standardized regression coefficients (b_3) against species abundances (number of individuals at plot level). Twenty species with identical initial size distributions and log-series abundances were simulated in a random spatial pattern. Note that in the panels of the bottom row, the number of neighbours was log-transformed. Data points are means (\pm 1 SD) from five replicate simulations. The simulated input value of β_3 (dotted lines) was -0.05 (top left) and -1.3 (bottom left). Continuous lines indicate significant ($P < 0.05$) positive (blue) or negative (red) regressions.

Figure. 3. Frequency distributions of number of conspecific neighbours within neighbourhood radius r (20 m) for individuals of rare ($n = 132$) and common ($n = 2827$) species in simulated communities with random spatial patterns. Note that the x-axis in the panels of the top row have identical scales. This is also true for the panels of the bottom row. Moreover, the number of conspecific neighbours was log-transformed in the panels of the bottom row. SD indicates the standard deviation of each distribution.

Figure. 4. Regressions of conspecific negative density dependence (regression coefficient, β_3 in Eq. 3) and species abundances (plot level basal area). Twenty species with identical initial size distributions and log-series abundances were simulated without, linear (1/distance) or squared (1/distance²) distance decay of conspecific neighbour effects within 20 m radius in random or aggregated spatial patterns. Data points are means (± 1 SD) from five replicate simulations. The simulated input value of β_3 was -0.2 (green line).

Figure. 5. Regressions of variation in conspecific neighbour density (expressed as SD in basal area of bigger conspecifics, ba_{CON} within 20 m) and species abundances (plot level basal area). Twenty species with identical initial size distributions and log-series abundances were simulated with random or aggregated spatial patterns without, linear (1/distance) or squared (1/distance²) distance decay of conspecific neighbour effects. Data points are means (± 1 SD) from five replicate simulations. Continuous lines indicate significant ($P < 0.05$) negative (red) or positive (blue) regressions.

Figure. 6. Regressions of effect sizes (squared partial correlation coefficients of β_3 in Eq. 3) and species abundances (plot level basal area). Twenty species with identical initial size distributions and log-series abundances were simulated with random or aggregated spatial patterns without, linear (1/distance) or squared (1/distance²) distance decay of conspecific neighbour effects within 20 m radius. Data points are means (± 1 SD) from five replicate simulations. Continuous lines indicate significant ($P < 0.05$) positive (blue) or negative (red) regressions.

Figure. 7. Regressions of standardized regression coefficients (b_3) and species abundances (plot level basal area). Twenty species with identical initial size distributions and log-series

374 abundances were simulated with random or aggregated spatial patterns without, linear
375 (1/distance) or squared (1/distance²) distance decay of conspecific neighbour effects within
376 20 m radius. Data points are means (\pm 1 SD) from five replicate simulations. Continuous
377 lines indicate significant ($P < 0.05$) positive (blue) or negative (red) regressions.

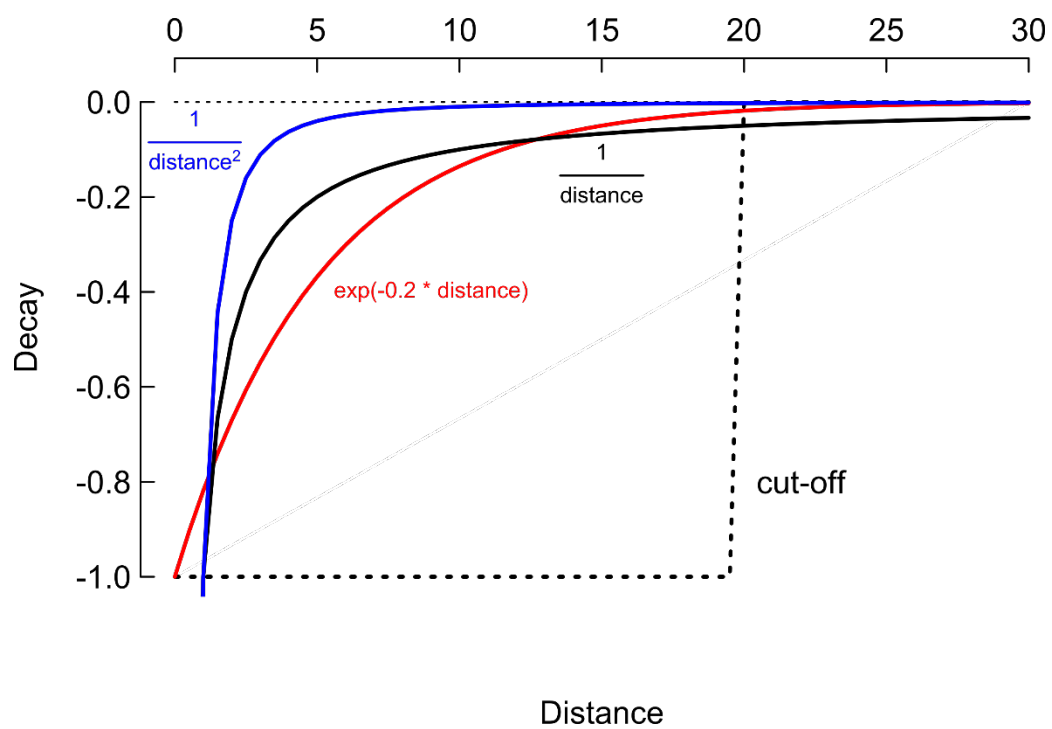


FIG. 1.

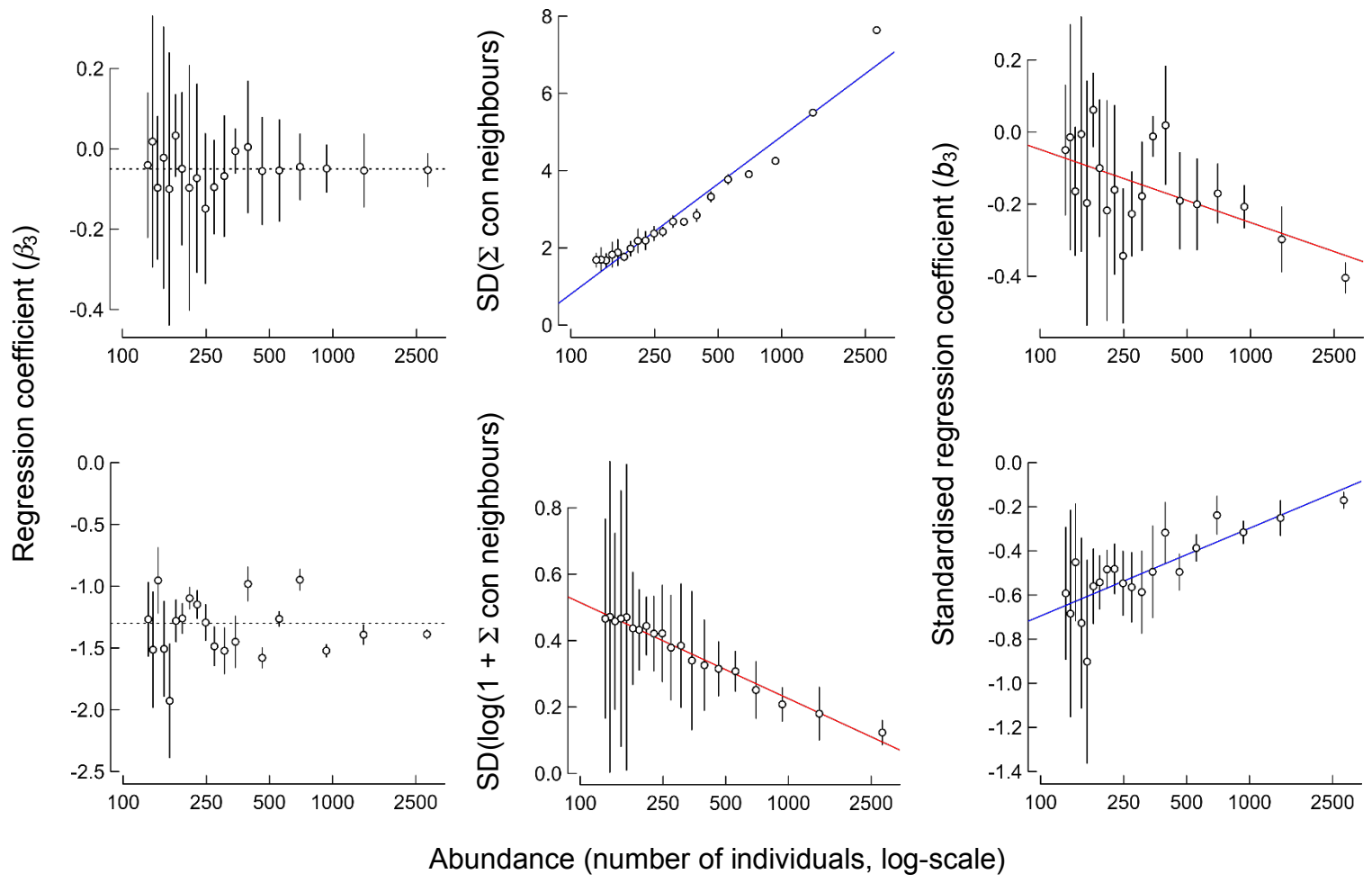


FIG. 2

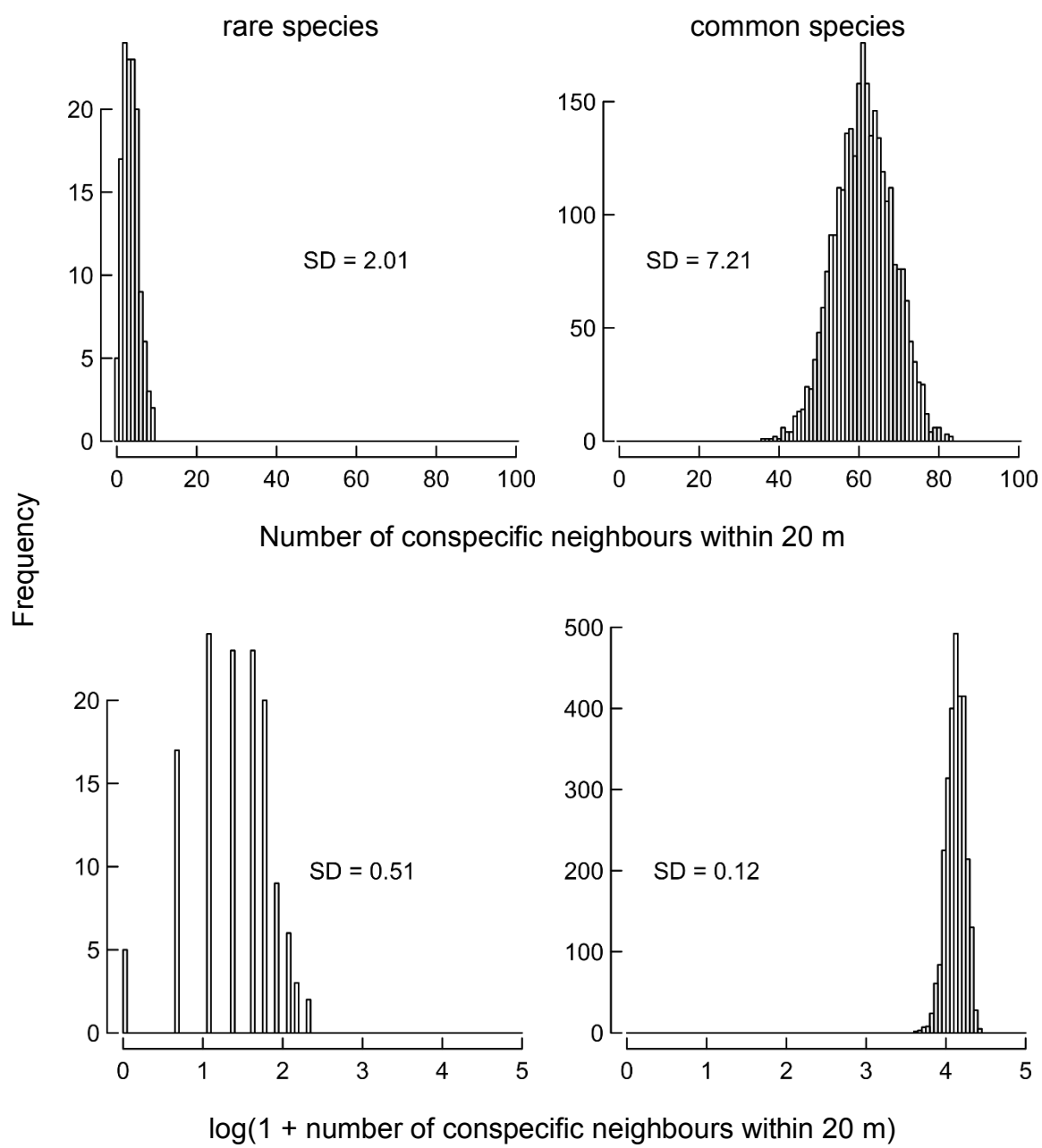


FIG. 3

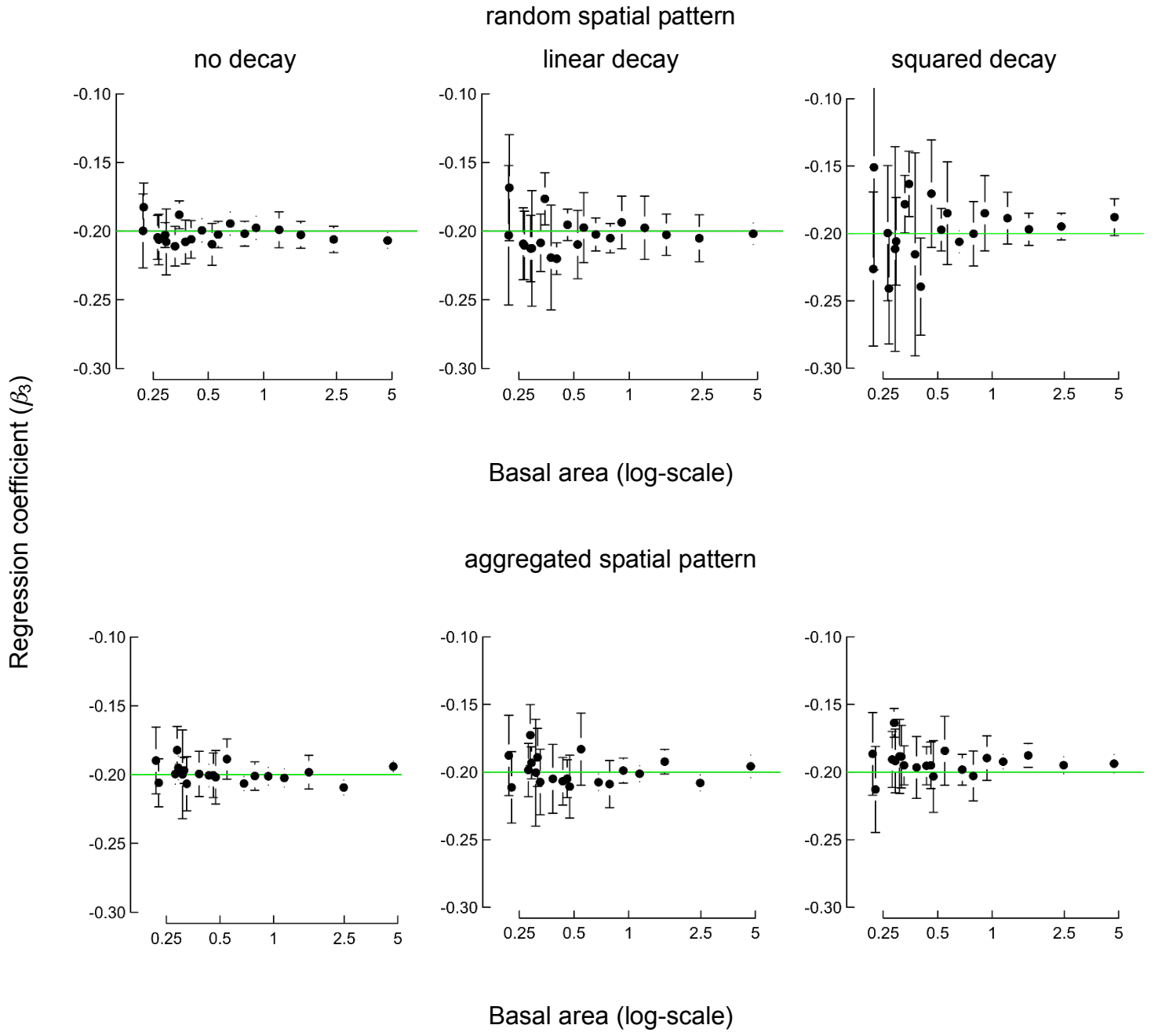


FIG. 4.

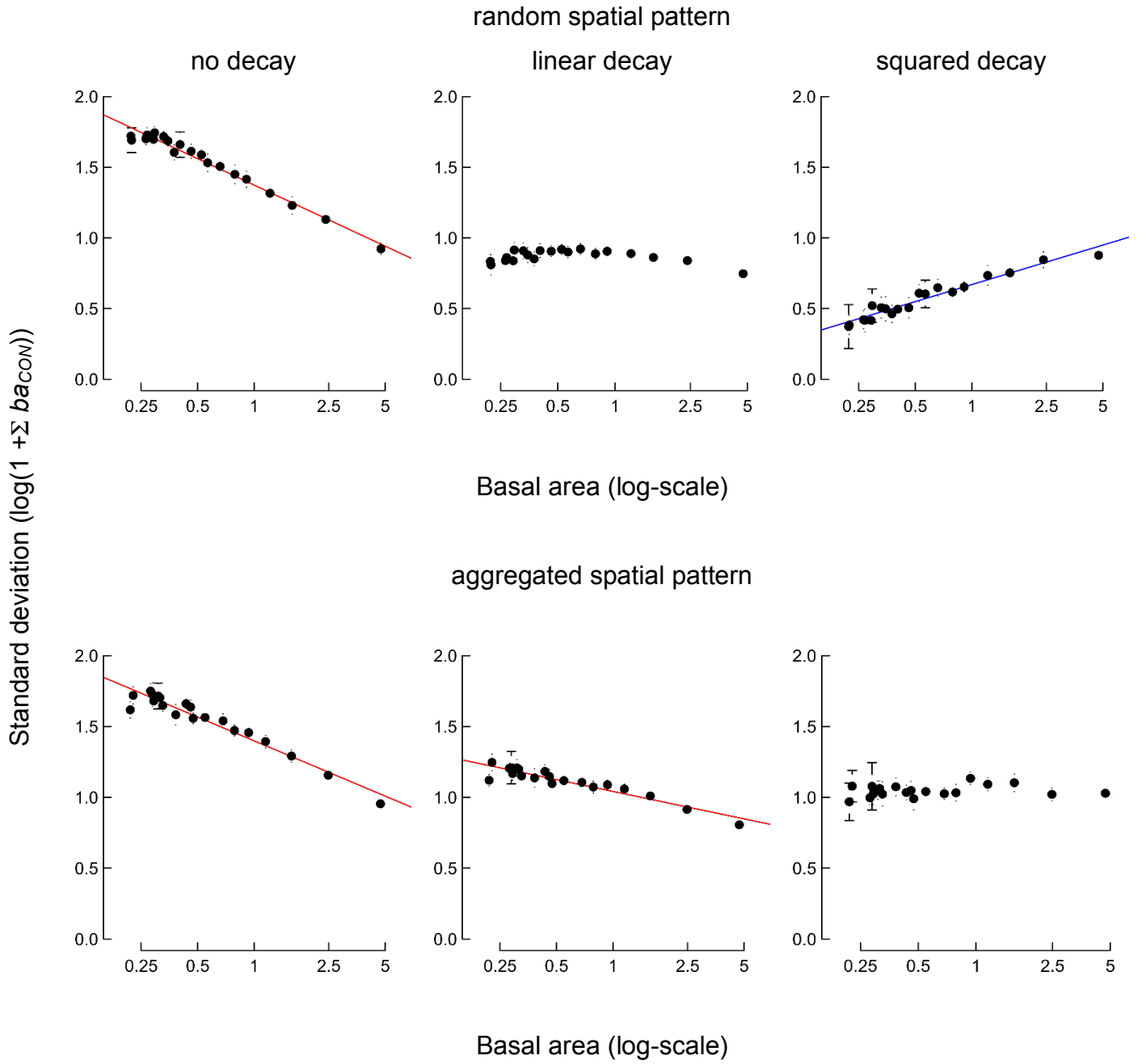


FIG. 5.

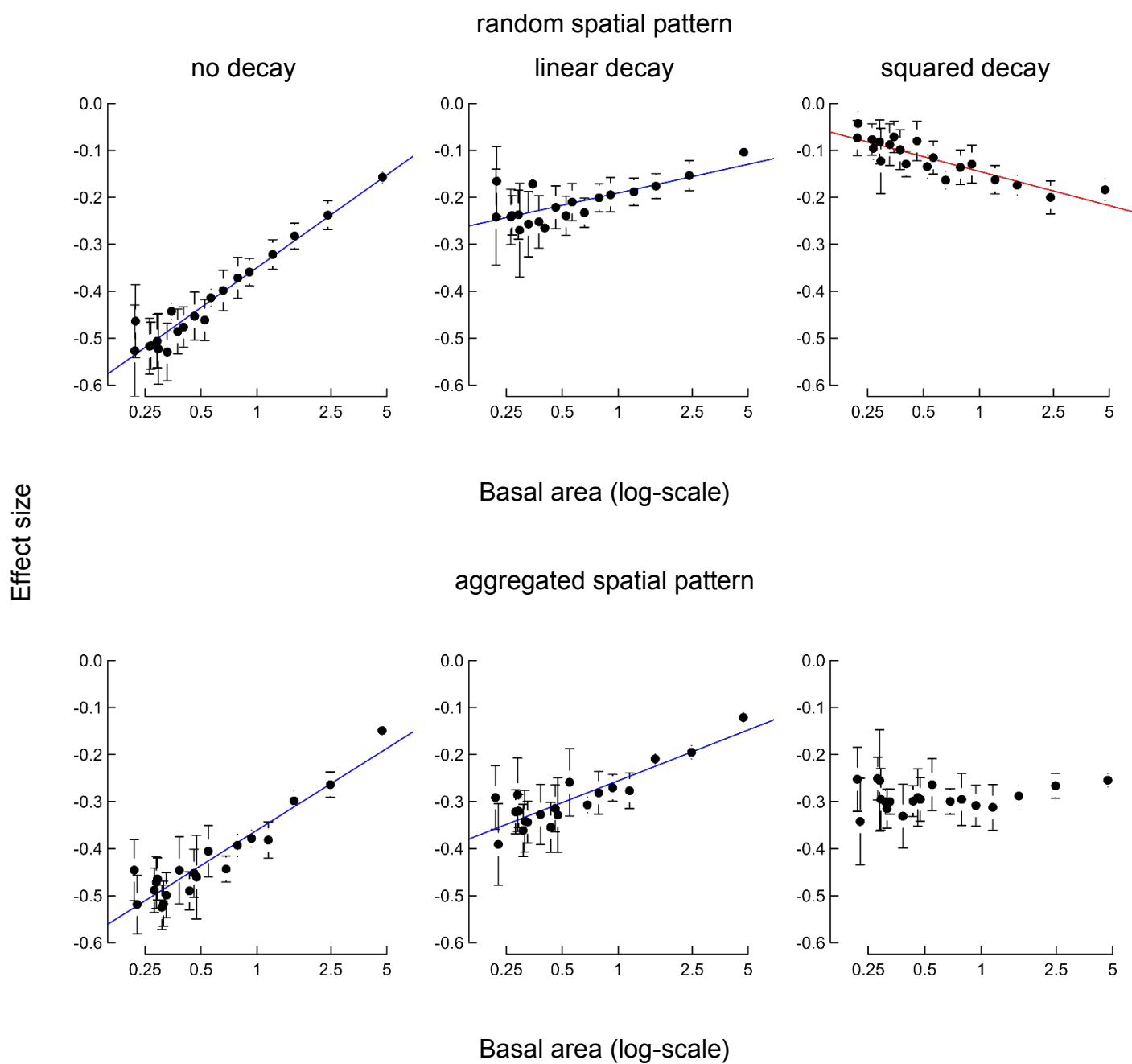


FIG. 6.

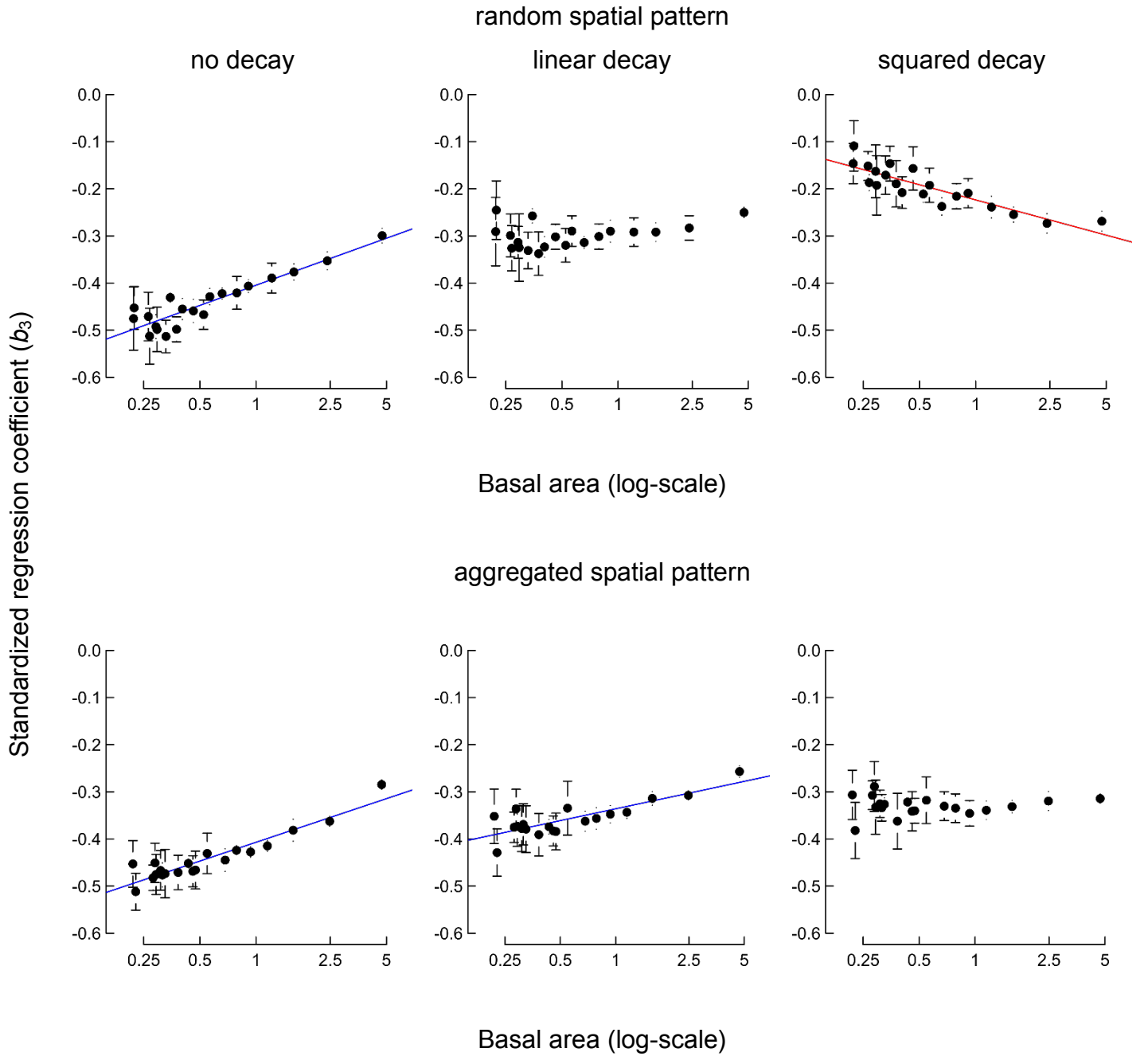


FIG. 7.